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An overview of the direct and indirect effects of acid rain on plants: Relationships among acid rain, soil, microorganisms, and plants

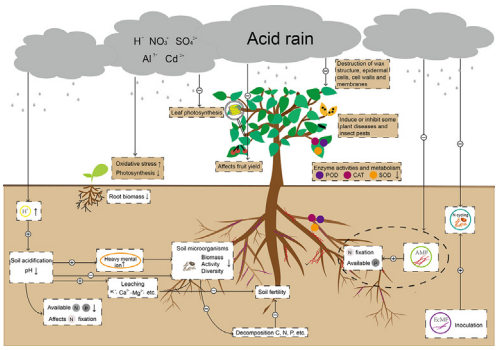
Yan Zhang [a], Jiahong Li [b], Junyan Tan [a], Wenbin Li [c], Bhupinder Pal Singh [d], Xunan Yang [e], Nanthi Bolan [f,g], Xin Chen [a], Song Xu [a], Yanping Bao [a], Daofei Lv [a], Anan Peng [a], Yanbo Zhou [a], Hailong Wang [a,h,*]

[a] School of Environmental and Chemical Engineering, Foshan University, Foshan 528000, China
[b] School of Karst Science, Guizhou Normal University, Guiyang 550001, China
[c] Key Laboratory of the Ministry of Education for Coastal and Wetland Ecosystems, College of the Environment & Ecology, Xiamen University, Xiamen 361102, China
[d] University of New England, School of Environmental and Rural Science, Armidale, NSW 2351, Australia
[e] Guangdong Provincial Key Laboratory of Microbial State Key Laboratory of Applied Microbiology Southern China, Institute of Microbiology, Guangdong Academy of Sciences, Guangzhou 510070, China
[f] UWA School of Agriculture and Environment, The University of Western Australia, Perth, WA 6009, Australia
[g] UWA Institute of Agriculture, The University of Western Australia, Perth, WA 6009, Australia
[h] Institute of Eco-environmental and Soil Sciences, Guangdong Academy of Sciences, Guangzhou 510650, China

HIGHLIGHTS

- Acid rain affects plant by regulating plant-associated soil microorganisms.
- Acid rain harms plant by inducing soil acidification and nutrient deficiency.
- Plant mycorrhizal types mediated the effects of acid rain on plants.

GRAPHICAL ABSTRACT



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ABSTRACT

Acid rain (AR) causes numerous environmental problems and complex negative effects on plants globally. Many studies have previously reported on direct effects of AR or its depositional substances on plant injury and performance. However, few studies have addressed the indirect effects of AR on plants as mediated by soil microorganisms and the abiotic environment of the soil rhizosphere. The indirect effects (e.g., AR → soil microorganisms→plants) need greater attention, because acidic deposition not only affects the distribution, composition, abundance, function, and activity of plant-associated microorganisms, but also influences the dynamics of some substances in the soil in a way that may be harmful to plants. Therefore, this review not only focused on the direct effects of AR on plant performance, growth, and biomass allocations from a whole-plant perspective, but also addressed the pathway of AR–soil chemical characteristics-plants, which explains how soil solute leaching and acidification by AR will reduce the availability of essential nutrients and increase the availability of heavy metals for plants, affecting carbon and nitrogen cycles. Mainly, we evaluated the AR-soil microorganisms-plants pathway by: 1) synthesizing the potential roles of soil microbes in alleviating soil acidic stress on plants and the adverse effects of AR on plant-associated soil microorganisms; 2) exploring how plant mycorrhizal types affect the detection of AR effect on plants. The meta-analysis showed that the effects of AR-induced pH on leaf chlorophyll content, plant height, and plant root biomass were dependent on

* Corresponding author at: School of Environmental and Chemical Engineering, Foshan University, Foshan 528000, China.
E-mail address: hailong.wang@fosu.edu.cn (H. Wang).

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plant mycorrhizal types. Some possible reasons for different synergy between mycorrhizal symbiotic types and plants were discussed. Future research relating to the effects of AR on plants should focus on the combined direct and indirect effects to evaluate how AR affects plant performance comprehensively.

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1. Introduction

Acid rain (AR) pollution has led to frequent ecological disasters and economic loss worldwide since the beginning of the industrial revolution (Singh and Agrawal, 2008; Grennfelt et al., 2020). Generally, emissions from human activities, including those caused by coal burning, industrial production, and automobile exhaust, produce acidic substances such as sulfur dioxide (SO_2) and nitrogen oxides (NO_x) (Bolan and Hedley, 2003; Bolan et al., 2005a; Bolan et al., 2005b; Vahedpour and Zolfaghari, 2011; Yun et al., 2019). Naturally occurring events, such as forest fires caused by lightning, volcanic eruptions, and ocean foam, also produce sulfur oxides (SO_x), concentrated sulfuric acid (H_2SO_4), and other acidic substances (Abbasi et al., 2013; Behera and Balasubramanian, 2014; Ruiz-López et al., 2019). Acidic substances react with moisture in the atmosphere to produce acid precipitation; these chemicals may be transported long distances and reach the ground in the form of acid deposition through a process known as the formation of AR (pH < 5.6) (Shukla et al., 2013; Warren et al., 2017) (Fig. 1). Acid rain may cause the acidification of soils and aquatic ecosystems and reduce crop yields, resulting in a decline in forested habitats and leading to the corrosion of infrastructure (Singh and Agrawal, 2008).

Plants are essential for diversity and productivity in terrestrial ecosystems while serving as AR pollutants' main interceptors and receptors. Therefore, the response patterns of plants to AR can provide researchers with a scientific theoretical basis for addressing related issues while helping land managers to develop technical countermeasures used in the restoration and reconstruction of degraded ecosystems in areas affected by AR (Fu and Tian, 2006). The performance of plants is directly related to the acidity of AR (Fan and Wang, 2000; Du et al., 2017; Shi et al., 2021). Simulation experiments have demonstrated that the growth and development of above- and below-ground organs (leaf and root, respectively) of plants are suppressed in simulated AR (SAR) treatments (Shi et al., 2021); thus, photosynthesis and growth are reduced (Yao et al., 2016; Du et al., 2017; Pham et al., 2021). The direct effects of the acidity of AR and the indirect effects of soil chemical characteristics mediated by AR on plants are well studied (Singh and Agrawal, 2008; Shi et al., 2021).

A high frequency of AR significantly decreases soil microbial biomass, diversity, and activity (Liu et al., 2020a and 2020b; Liu et al., 2021a and 2021b). Microorganisms in the rhizosphere may affect the transformation of AR pollutants deposited in soil (Fujii, 2014); they may induce plants to secrete plant hormones, such as indoleacetic acid, that can regulate growth and reproduction (Lu et al., 2018) during AR stress. Microorganisms are an essential component in soils and play an important role in mediating the effects of AR on soil-plants system (Killham et al., 1983). However, the AR-soil microorganism-plant pathway was not well documented in the past. The majority of plant species form root symbioses with arbuscular mycorrhizal fungi (AMF), followed by ectomycorrhizal fungi (EcMF) (Soudzilovskaia et al., 2020), having dramatic consequences for plant growth and response to environmental stresses including AR. For example, the nitrogen (N) addition had been shown to have a negative effect on different AMF guilds moderated by soil pH (Han et al., 2020). Similarly, the EcMF colonization of roots is also known to be negatively affected by N deposition (Nilsson et al., 2007). However, symbiotic microorganisms in plants can alleviate many adverse effects of AR on plants including heavy

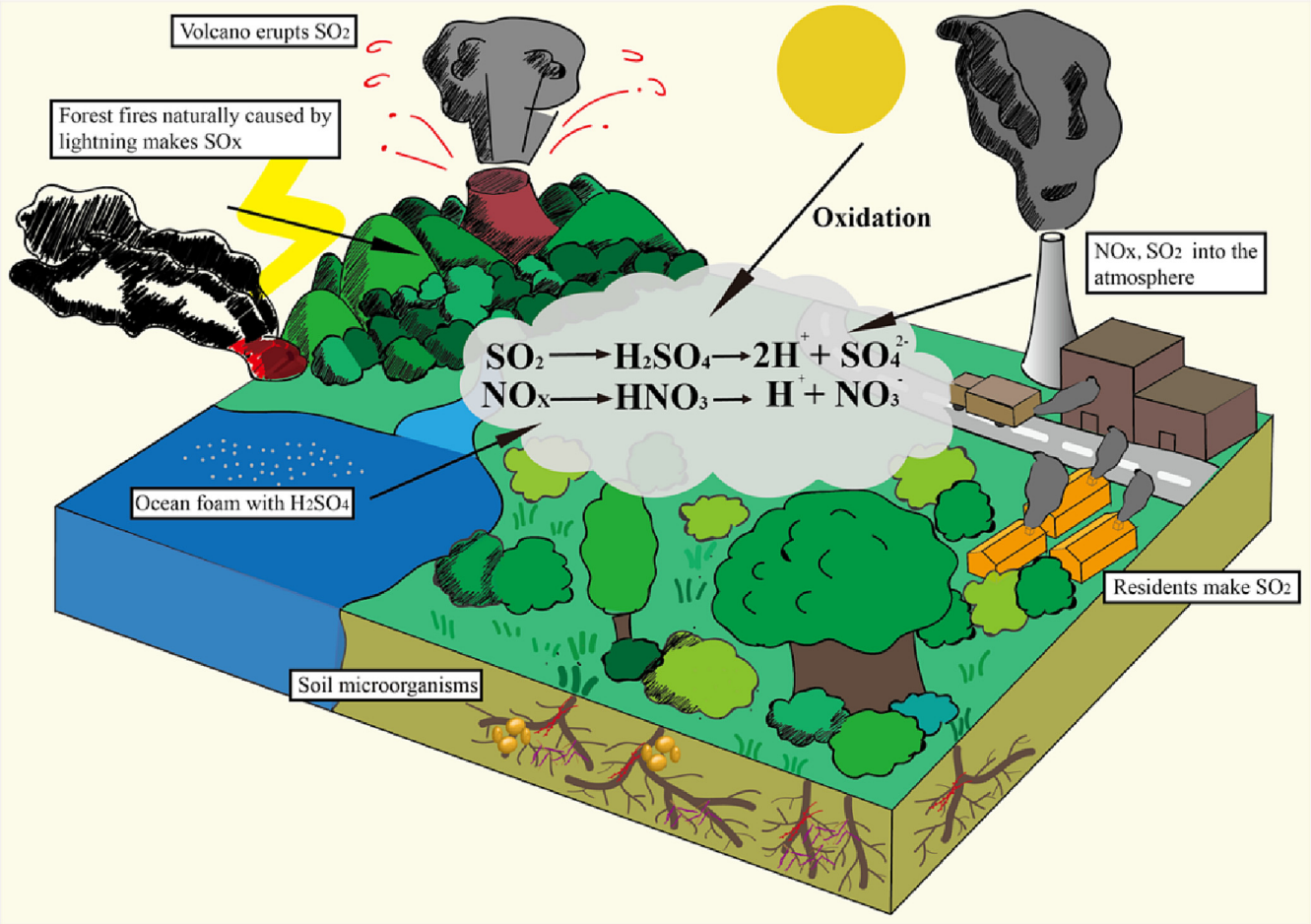

Fig. 1. Three-dimensional model of acid rain formation, including natural forces and human activities. Sulfur dioxide (SO_2), sulfur oxide (SO_x), sulfuric acid (H_2SO_4), nitrogen oxide (NO_x), and nitric acid (HNO_3).

metal toxicity, e.g., by inoculation of AMF (Meier et al., 2012; Xia et al., 2021) and EcMF (Hu et al., 2022). The negative effect of nitrogen deposition or acidic stress effects on plant-associated soil microbes has been well-documented by previous meta-analysis literatures (Treseder, 2008; Zhou et al., 2017; Zhang et al., 2018; Meng et al., 2019; Han et al., 2020), nevertheless, how plants vary in mycorrhizal types response to AR stress was less considered.

Here, we elaborated on the effects of AR by considering the direct and indirect effects of AR on soil-plant system simultaneously. In addition, meta-analysis was used to analyze the effects of different plant mycorrhizal types (such as arbuscular mycorrhizal (AM) and ectomycorrhizal (EcM) related plants) in mediating the effects of AR on plants.

2. Materials and methods

2.1. Literature search and review

A systematic literature search was conducted using the ISI Web of Science (isiknowledge.com) based on a topic search of titles, abstracts, and keywords. First, we searched the relevant literature following the direct and indirect relationships between AR and plants using the following topics for review: ("acid* deposition" OR "acid* rain" OR "acid* precipitation") AND ("growth" OR "biomass" OR "performance"). Second, we searched topics on microbe- or soil-mediated AR effects on plants using terms ("acid* deposition" OR "acid* rain" OR "acid* precipitation") AND ("*mycorrhizal fung*" OR "rhizobi*" OR "soil bacteri*" OR "soil fung*" OR "N-fixing bacteri*" OR "soil microb*"). We later conducted a supplementary search on the topic of sulfur or nitrogen related acid deposition effects on plant or plant-associated soil microbes by restricting the above terms using ("sulfur deposition" OR "nitrogen addition" OR "nitrogen enrichment" OR "nitrogen deposition" OR "nitrogen fertilization" OR "nitrogen input" OR "nitrogen application"). We included any studies that considered the following research aspects for the review: (1) Direct effects of AR on plant morphology or physiology traits or characters; (2) Soil acidification caused by AR that affects plants; and (3) The relationship between plant-associated microbes and plants and their mediated effects on AR was considered. The studies that met these criteria were discussed in the main text and listed as references.

2.2. Data collection

For the meta-analysis, we followed the procedure known as Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) to screen our records. The studies included in our meta-analysis satisfied the following criteria: (1) At least one plant morphology, physiology trait, or character should be reported; (2) The studies should conduct an AR experiment with pH gradients by simulating either sulfuric acid rain, nitric acid rain or mixed acid rain; (3) For papers on N and S deposition, specific pH value should be provided; and (4) Sample sizes and means for the control and treatment groups were accessible in the texts, figures, or supplementary materials of the analyzed documents. A total of 33 articles met our criteria in the meta-analysis after PPRISA was conducted (Fig. S1). Data from figures were extracted using the Engauge Digitizer software (https://github.com/markummitch ell/engauge-digitizer). We filled unavailable standard deviations using the "metagear" package in R software

(Lajeunesse, 2016a). The pH of both naturally observed AR and simulated AR treatments ranged from 1 to 5.6 (Table S1).

2.3. Meta-analysis

We treated AR gradient, plant growth form, and mycorrhizal type as moderators to examine their effects on each plant growth-related trait or character (Table S1). The effect size for each plant trait or character variable was estimated based on the natural log-transformed response ratio lnRR = ln (Xe / Xc), where Xe was the experimental treatment mean and Xc was the control mean. The variance associated with each value of lnRR was calculated from the standard deviation (SD) related to each decomposition value. If only standard error (SE) was reported in the studies, we converted it into SD. We used meta-analysis with multi-level random effects and included paper ID and species ID (species list was shown in table S2) as random factors.

Firstly, we performed random effect meta-models to calculate the overall mean effect size of AR on each variable. Secondly, we incorporated moderators and their interactions with AR gradients in the meta-models. Only seed germination, leaf chlorophyll content, root biomass, and plant height were selected to explore the effects of moderators on plant responses to AR due to their larger sample sizes and better convergence in model fittings. For overall mean effect models, we investigated total, residual and random-effect specific relative heterogeneity (Table S3). All meta-models were fitted using "rma.mv" function in R package "metafor" (Viechtbauer, 2010). To direct present treatment effects by percentage change, the percentage changes were measured using [exp (lnRR) - 1] × 100 %, with 95 % confidence intervals (CIs) that did not overlap with zero, considered statistically significant. All data were analyzed using version R 4.1.0 (R Core Team, 2021).

We checked publication bias through a funnel plot with the "funnel" function in "metafor". We also performed the rank correlation test to examine the asymmetry of funnel plots by the "ranktest" function. When there was publication bias ($p < 0.1$), we calculated a fail-safe number to test the robustness of our results with the "fsn" function. The funnel plots and the rank correlation tests indicated possible publication bias in leaf chlorophyll content ($p = 0.04$) and plant height ($p = 0.004$) (Fig. S2). The fail-safe number indicated that the negative effects of leaf chlorophyll and plant height might be robust to publication bias (leaf chlorophyll content: 35008, required >385; plant height: 173284, required >290). Details and some results of the meta-analysis method were shown in the supplementary materials (Fig. S2 and Tables S3).

3. Direct effects of AR on plant morphology and physiology

3.1. Effects on plant leaf

3.1.1. Effects on leaf micromorphology

The effects of AR on leaf blade micromorphology include the destruction of the waxy structure on the surface and of epidermal cells, which may lead to a series of adverse effects on plant photosynthesis. For example, AR can lead to the collapse of the epidermis and deformation of stomata, as well as the partial collapse of spongy tissue (Chen, 2001; Sant'Anna-Santos et al., 2006; Andrade and Silva, 2017). Stomata serve as the main channel for gas exchange in plants, and the destruction of stomatal function will lead to adverse effects on plant growth and development. For example, at pH 3.0, Sant'Anna-Santos et al. (2006) observed that the epidermal and mesophyll cells of *Genipa Americana* leaves begin to shrink; the spongy tissue cells experienced hypertrophy before which phenolic substances and starch granules accumulate.

3.1.2. Effects on organelles in leaf

Acid rain can disrupt organelles and mesophyll tissue in leaves, damaging organelles such as chloroplasts and mitochondria. For example, AR can destroy cell walls and cell membranes, forming mitochondrial ridges between larger inclusions (Chen et al., 2017). Additionally, AR can lead to the deformation of chloroplasts and disorder in the arrangement of thylakoid membranes, ultimately causing crests to disappear, decreasing the chlorophyll content, and limiting the number of chloroplasts available for photosynthesis (Ferenbaugh, 1976; Hindawi et al., 1980; Lan et al., 2019).

3.1.3. Effects on leaf photosynthesis

When an AR treatment lowered the pH, leaf chlorophyll content was shown to decline significantly (Fig. 3a and Table S4), directly impeding photosynthesis (Gao et al., 1997) and hampering the accumulation of plant organic matter (Sun et al., 2016). In addition, negative effects on leaves from AR include eroding wax on the leaf surface, damaging chloroplasts and acid-induced base cation leaching in mesophyll cells (Dong et al., 2017) (Fig. 2(1)).

The effects of AR on plant photosynthesis are related to specific plant taxa, life history stages, and treatment pH levels (Liu and Cao, 1993; Yan et al., 1999; Wu et al., 2004). It was noticed that leaf chlorophyll content increased as treatment pH increased (Fig. 3a and Table S4). Additionally, the leaf chlorophyll content of both woody and non-woody plants decreased as AR treatment pH decreased (Fig. 4a). Non-woody plants were found to be more sensitive to AR than woody plants, as the slope of log response rates dropped more steeply under low treatment pH (Fig. S3a), which might be due to the difference in the characteristics of leaf surfaces between woody and non-woody plants (Sant'Anna-Santos et al., 2006; Singh and Agrawal, 2008; Du et al., 2017). In addition, AR may positively affect the leaf photosynthetic rate when the foliar uptake of nitrates from acid rainwater occurs (Dong et al., 2017), and woody plants may benefit from the fertilization effect (Shi et al., 2021). The AR had an overall negative effect on the leaf chlorophyll content of plants that have a symbiotic relationship with arbuscular mycorrhizal fungi (AM plant) (Fig. 4a), and leaf chlorophyll content of both AM and EcM plants improved in increasing acid treatment pH (Fig. 5a).

Other mechanisms are involved when AR affects the photosynthetic rate, including swaying the transcription and activity of chloroplast ATPase, altering cell acidity, or restricting the antioxidant defense system, leading to metabolic disorders (Zhang et al., 2020a).

3.1.4. Effects on enzyme activities and metabolism in leaves

Acid rain has been shown to cause a series of alterations in plant membrane permeability, enzymatic activities, synthesis of free radical antioxidants, and metabolism (Zhang et al., 2011; Xalxo and Sahu, 2017; Ren et al., 2018; Ma et al., 2020). Plants have systems designed to remove free radicals including reactive oxygen species (ROS) through both non-enzymatic and enzymatic pathways. Superoxide dismutase (SOD) is the first line of defense against antioxidants. Catalase (CAT), the second line of defense, involves scavenging H_2O_2, which is produced in the cell (Gajewska and Skłodowska, 2008). Peroxidases (POD) can protect cells from high ROS concentrations (Ju et al., 2017).

These enzymatic systems can protect the structure and function of cells as well as maintain the redox status of cells (Ren et al., 2018). However, AR would affect the SOD, POD, and CAT of plant leaves (Fig. 2(2)). The SOD activity of spinach leaves was found to decrease with increasing acidity caused by AR (Liu and Cao, 1993). Another study showed that the activities of SOD, POD, and CAT initially rose in wheat and then fell with a decrease in the pH of AR, showing a hump-shape curve (Yan et al., 1999). Thus, low pH treatment of SAR might affect and perturb the defense mechanisms of plants, which in turn increases membrane permeability (Ren et al., 2018) based on the ability of a plant species to tolerate AR stress (Zhang et al., 2011).

In addition, AR can generate some changes in metabolic conditions. Nitrate reductase plays an essential role in the N metabolism of plants and is related to the uptake and use of N by plants (Qi et al., 2001). Increasing AR intensity and treatment duration decreased nitrate reductase levels in plants (Solomonson and Spehar, 1977).

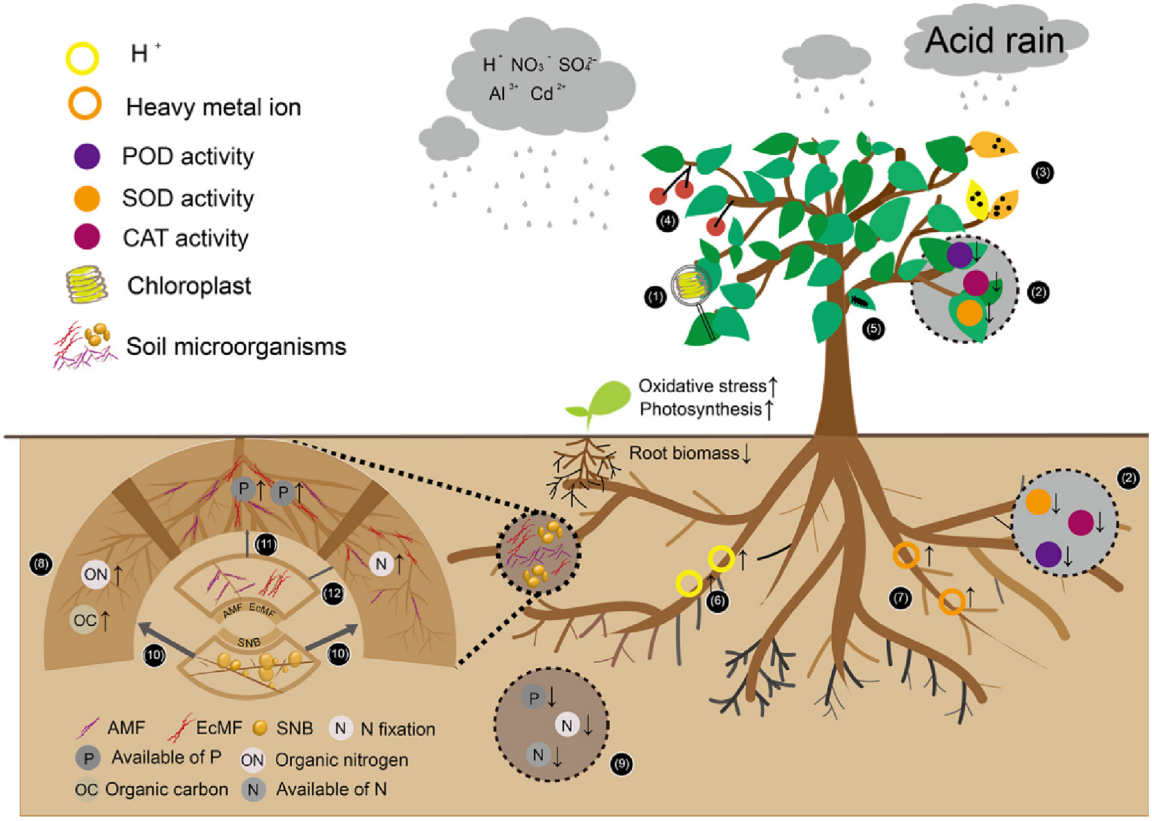

Fig. 2. The mechanisms of how acid rain (AR) affects plants; effects on: (1) leaf photosynthesis (e.g., destruction of leaf chloroplast); (2) enzyme activities and metabolism in leaves (e.g., affecting microorganisms, superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT)); (3) leaf lesions (e.g., some symptoms of the damage, such as yellow-brown and black-brown necrotic spots); (4) plant reproduction; (5) AR induced plant diseases and insect pests; (6) hydrogen ions (H^+) leaching into soils; (7) soil salt leaching (e.g., the heavy metal ions); (8) accumulating of organic carbon (OC) and organic nitrogen (ON); (9) affecting the absorption of available phosphorus (P) and nitrogen (N); (10) the effects of soil nitrogen-fixing bacteria (SNB) on nitrogen cycling; (11) the effects of arbuscular mycorrhizal fungi (AMF) on the absorption of available P and (12) the effects of ectomycorrhizal mycorrhizal fungi (EcMF) on the absorption of available N.

3.1.5. Apparent damage to plant leaves

The micromorphological and internal physiological changes of leaves exposed to AR manifest apparent characteristics in these phenomena (Sant'Anna-Santos et al., 2006). The leaves will show some symptoms of damage, such as yellow-brown and black-brown necrotic spots at the margin and between the veins, excessive greenness, curl, wilting (Fig. 2(3)), and even abscission during or after AR treatment (Fan and Li, 1999; Dursun et al., 2002; Kohno, 2017).

Thresholds of apparent AR damage for woody and non-woody plants become obvious below pH 5. A simulated AR (SAR) treatment at pH 2.5 caused necrotic spots on the leaf surfaces of *Camellia sinensis* (Zhang et al., 2020b). The oldest leaves showed several changes, such as small brown spots with an SAR of pH 3.0 (Wyrwicka and Skłodowska, 2006; Singh and Agrawal, 2008). When treated with SAR of pH 2.0, half of the tested ornamental herb species had lesions, which covered >20 % of the leaf area (the percentage of leaf injury ranged from 30 to 65 %). However, some plants, such as *Brassica oleracea* var. *acephala*, *Viola tricolor*, and *Zephyranthes candida*, were found to be highly resistant to AR (Zhang et al., 2007). It was concluded that leaves exhibited the following alterations in response to AR: (1) wilting of common epidermal cells and structural damage of stomatal guard cells under pH 4.5, (2) interveinal and marginal necrotic dots, (3) flaking of epicuticular wax, (4) turgor loss, (5) epidermal cell shape modification, (6) hypertrophy of parenchymatous cells, (7) collapse of epidermal and mesophyll cells under pH 3.0, (8) necrotic spots, (9) cuticle changes, and (10) areas of total tissue destruction under pH 2.5 (Andrade and Silva, 2017; Andrade et al., 2020; Rodríguez-Sánchez et al., 2020; Zhang et al., 2020b).

The AR-induced apparent changes in plants were caused not only by the difference in the pH of AR but also by the differences in morphological, structural, and biological characteristics of each plant species (Qi et al., 2004; Li et al., 2011). For example, the leaves of the fern species *Pteridium aquilinum* are sensitive to SAR treatments. In contrast, *Quercus palustris* species and a woody species with thicker leaves are insensitive to SAR treatments, with <1 % of the leaf area damaged. Other factors, such as rainfall intensity and duration of AR treatment, affect the amount of damage caused to leaves (Fan et al., 1999; Zhang et al., 2007).

3.2. Effects on plant growth

3.2.1. Effects on plant above/belowground length

Plant height or stem height has often been shown to decrease with a decrease in AR treatment pH (Figs. 2(6) and 3b and Table S5–S6). The height of both woody and non-woody plants tends to decrease under low pH treatment (Fig. 4b). The increase in the height of woody plants under a high AR treatment pH was found to be not significantly different from that of non-woody plants (Fig. S3b). The height of plants that had a symbiotic relationship with arbuscular mycorrhizal fungi (AM plant) or had a facultative symbiotic relationship with ectomycorrhizal fungi and arbuscular mycorrhizal (EcM-AM plant) was found to decrease under low pH (Fig. 4b). However, the height of all mycorrhizal type plants was positively correlated with the treatment pH gradient (Fig. 5b). In addition, the underground parts of plants were affected by AR. Under the stress of low AR treatment pH, plant roots might appear hollow and sparse. Plant root length may decrease as the treatment pH of SAR decreased (Fig. 3d).

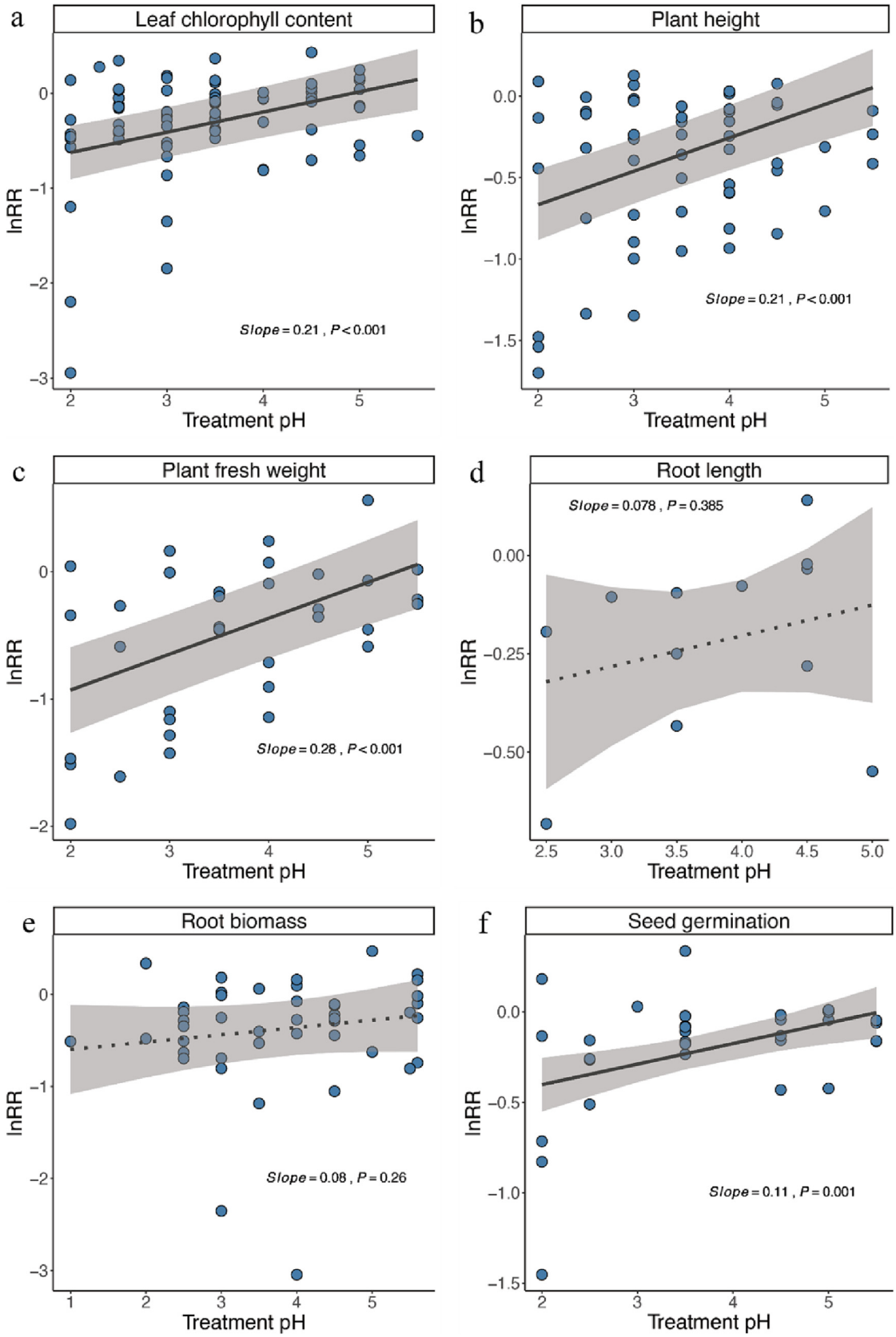

Fig. 3. Effects of acid rain on (a) leaf chlorophyll content, (b) plant height, (c) plant fresh weight, (d) root length, (e) root biomass, and (f) seed germination (only woody species). Shaded areas are 95 % confidence intervals. Solid and dotted lines denote significant ($p < 0.001$) and insignificant ($p < 0.1$) relationships, respectively.

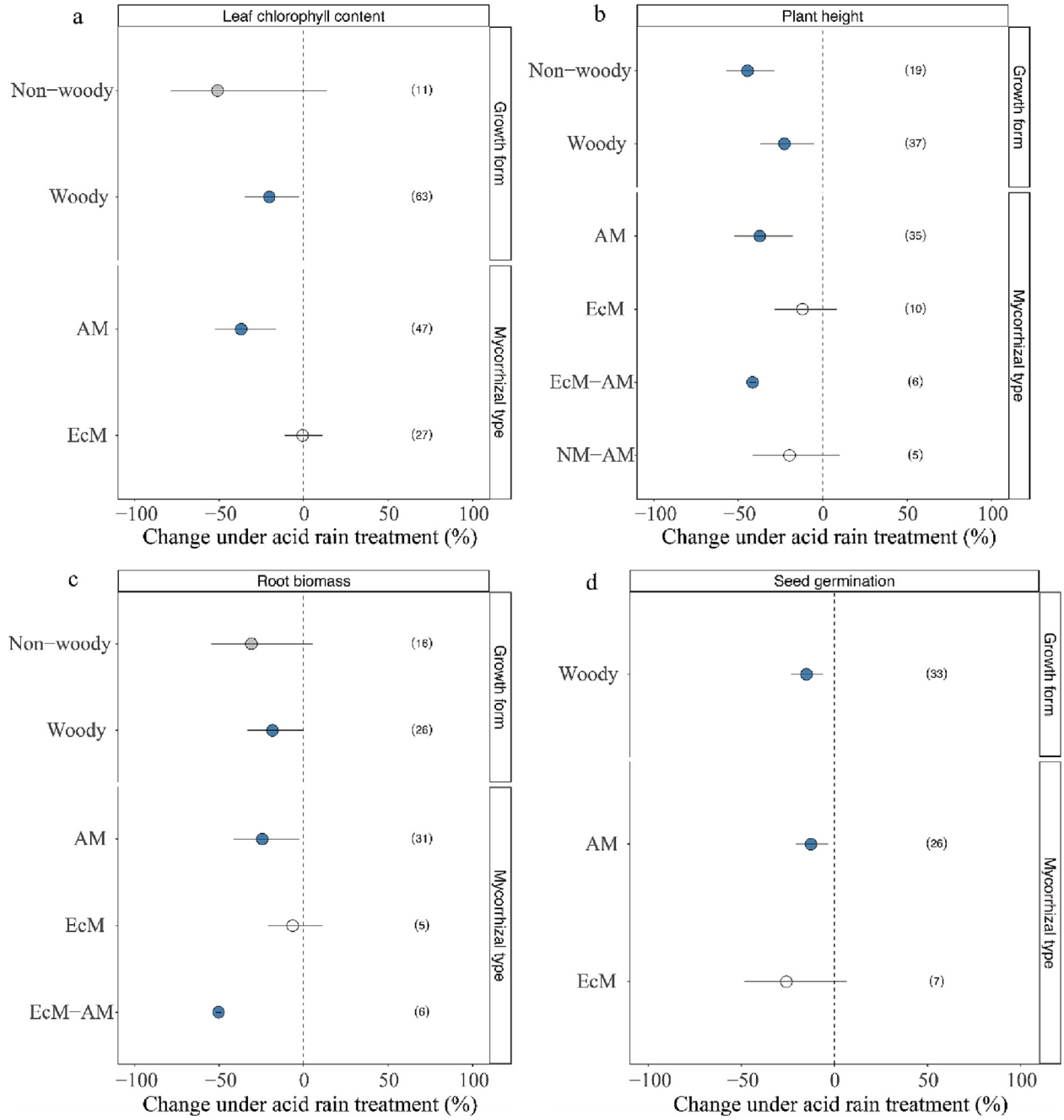

Fig. 4. Effects of acid rain on (a) leaf chlorophyll content, (b) plant height, (c) root biomass, and (d) seed germination (only woody species) about categorical moderators. Numbers in parentheses indicate the sample size. The percentage of changes with 95 % confidence intervals that did not overlap (blue points), marginally overlapped (grey points), and overlapped (white points) with zero was considered statistically significant ($p < 0.01$), marginally significant ($p < 0.1$), and insignificant ($p > 0.1$), respectively. Plant mycorrhizal types included arbuscular mycorrhizal (AM), ectomycorrhizal mycorrhizal (EcM), ectomycorrhizal-arbuscular mycorrhizal (EcM-AM), and non-mycorrhizal fungi or arbuscular mycorrhizal fungi (NM-AM) types.

3.2.2. Effects on above/belowground weight

The total biomass and its allocation in plant organs reflect the strategy a plant employs to capture resources, manage biotic and abiotic stress, biomass partitioning, and the species' function in a plant community (Dovrat et al., 2019). Plants have a remarkable ability to coordinate organ growth; thus, a tight balance exists between above ground (i.e., stem) and below ground (i.e., root) biomass production (Poorter and Nagel, 2000). First, plant fresh weight refers to the mass of a plant's cells under normal living conditions. Because AR destroys plant cells and causes a large amount of water loss, generally, the fresh weight of most plants drops with decreasing pH under SAR treatment (Figs. 2(7) and 3c and Tables S7–S8).

Low pH levels of SAR were shown to reduce the photosynthetic ability of plant leaves (as shown in Section 3.1.3), leading to a smaller allocation to root formation (Okon and Akpan, 2014). Fine root biomass is significantly reduced with the decrease in the pH of AR (Liu et al., 2018). We found the effects of SAR on root biomass were variable (Table S7); and the overall effect was insignificant (Fig. 3e), although both woody and non-woody species were vulnerable to a decrease in pH of AR treatment (Figs. 4c and S3c).

Plant root biomass varied in response to AR treatment between plant symbiotic functional groups (Figs. 4c and 5c). The root biomass of AM and EcM-AM plants was found to decrease under SAR treatment (Fig. 4c).

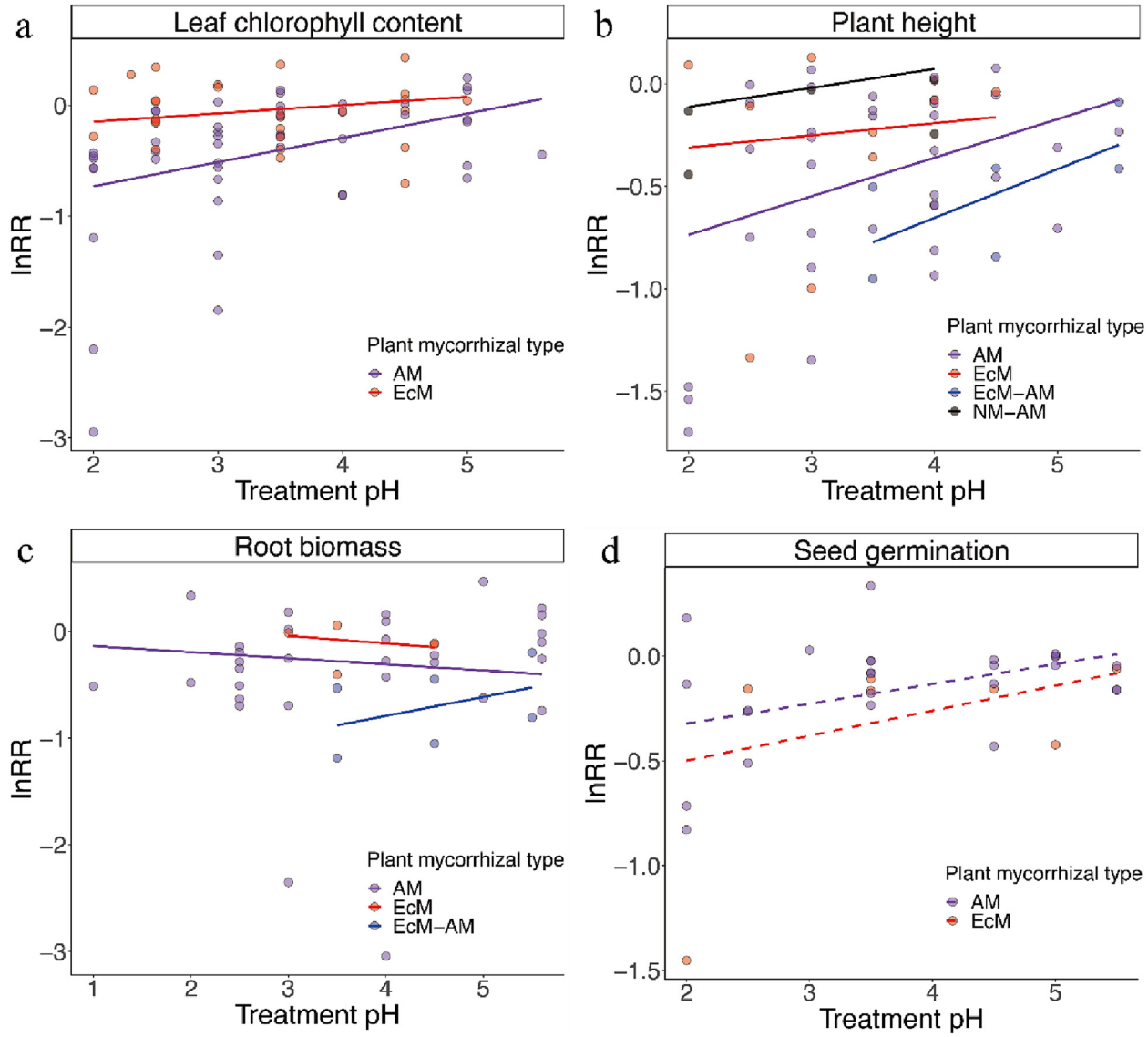

Fig. 5. Interactive effects of plant mycorrhizal types with AR acidity on (a) leaf chlorophyll content, (b) plant height, (c) root biomass, and (d) seed germination (only woody species). Solid and dashed lines denoted significant interaction ($p < 0.01$) and insignificant interaction ($p > 0.1$) from the random effect meta-model, respectively. The interaction of plant mycorrhizal types (arbuscular mycorrhizal (AM), ectomycorrhizal-arbuscular mycorrhizal types (EcM-AM), and non-mycorrhizal-arbuscular mycorrhizal types (NM-AM) with acidity gradients was estimated relative to the interaction of ectomycorrhizal mycorrhizal types (EcM) with acidity gradients.

The interaction of symbiotic type and acidity showed that the root biomass of EcM and AM plants reduced with increasing pH; in contrast, it increased in EcM-AM plants at a higher pH (Fig. 5c). These results may be related to the differences in the synergy between plant and fungal types (Emmanuel and Babalola, 2020) and may indicate that AM and EcM fungi may function in alleviating the negative effect of AR on root mass allocation under low pH. Some possible reasons for different synergy between different mycorrhizal types and plants include: Firstly, some mycorrhizal types are more suitable than others to form a special symbiotic relationship with plants. For example, AM fungi can effectively promote plant nutrient uptake, particularly phosphorus, and plant biomass accumulation (Bolan, 1991; Mohammadi et al., 2011). This characteristic may make it easier to develop favorable symbiotic relationships with plants regarding root biomass. Secondly, the different environmental adaptability in mycorrhizal type also has certain influence. For instance, soil environmental stress may affect the survival rate of AM fungi depending on mycorrhizal guilds (Han et al., 2020), thus affecting the synergy with plants (Herrera-Peraza et al., 2011). However, AM fungi can alter biochemical properties of plants to better cope with environmental stress (Mohammadi et al., 2011; Meier et al., 2012).

In addition, the AR causes an acceleration of the leaching of base cations such as calcium (Ca), magnesium (Mg), and potassium (K) from leaves (Ju et al., 2017), and a further reduction in plant total biomass may occur (Zhang et al., 2016; Diatta et al., 2021).

3.3. Effects on plant reproduction

Generally, AR affects plant flowering, fruit yield, and reproduction (Fig. 2(4)). Petals are more sensitive to acid solutions than leaves (Kohno, 2017), which may impede flower development. For example, SAR was found to delay chrysanthemum flowering and reduce the total number of chrysanthemum buds (Kumar, 2016), and the core petals faded when the pH fell below 3.5. However, moderate AR tended to increase plant biomass yields owing to the fertilization effect (Neufeld et al., 1985). When the pH of SAR reaches the optimal value for plant growth, it can stimulate the growth of crops to a certain extent while increasing crop productivity (Evans and Curry, 1979).

Seed germination and seedling growth are bottleneck conditions related to the early establishment of plants. These early stages require enough

water to promote radicle germination and subsequent seedling growth. Germination begins with a passive hygroscopic process, followed by the expansion of existing tissue, rupture of the seed coat, and finally, the division of embryonic cells and tissue extension (Rajjou et al., 2012; Penfield, 2017). Low pH in an SAR treatment was found to decrease the seed germination rate (Fig. 3f and Table S9). Additional analysis showed that the seed germination of AM plant was significantly reduced under AR (Fig. 4d); however, the acidity of AR did not interact with plant mycorrhizal types (Fig. 5d). Other studies on non-woody species imply a pH below 2.5 may inhibit all seed germination (Wang et al., 2008).

Plant seedlings vary in species response to AR depending on the pH level. Seedlings of *Trichilia dregeana* showed physiological and chemical stress symptoms associated with acid deposition below pH 3.0 (Ramlall et al., 2015). In a study on the growth response of three legumes (*Vicia faba*, *Phaseolus multiflorus,* and *Pisum sativum*) to SAR, the results showed that SAR at pH 5.6 and pH 4.5 promoted the growth of seedlings. In contrast, AR at pH 2.5 and pH 3.5 inhibited the growth of seedlings of these species (Ashenden and Bell, 1989). Under SAR stress at pH 3.5, the growth of Chinese fir seedlings was seriously hindered (Fan et al., 2005). Mulberry (*Morus alba*) seedlings had a high tolerance to SAR at pH 4.5 (Zhang et al., 2020c), and *Pinus massoniana* might resist an acidic environment at pH 4.5–5.6 (Zhou et al., 2020). These results imply that many seedlings of plant species may tolerate SAR when the pH treatment is above an approximate threshold (e.g., pH 3.5).

3.4. AR-induced plant diseases and insect pests

When AR destroys the epidermal and plasma membrane cells of leaves, the ability of the leaf to protect itself decreases, allowing pathogens, bacteria, and fungi to invade and harm the leaves (Fig. 2 (5)). However, the relationships between AR, plant diseases, and insect pests may be complex. The damage caused by AR provides a convenient pathway for disease and insect infection, while AR can also inhibit some plant diseases and insect pests and thus reduce their spread. For example, when a tomato plant was initially treated with SAR, plant diseases can be aggravated by the inoculation of infectious bacteria after the initiation of leaf spot. If the bacteria are initially experimentally inoculated first and then plants are treated with SAR, some diseases can be alleviated because AR can inhibit the growth of infectious bacteria (Bisessar et al., 1984). A pH 3.5 treatment can dramatically extend the incubation period of wheat yellow rust disease, reducing sporulation and decreasing the area under a disease progress curve (Wang et al., 2018).

4. Indirect effects of AR on plants

4.1. AR-soil chemical characteristics-plant

4.1.1. Excessive nitrogen deposition and hydrogen ions (H^+) leaching of soils

Acid rain has been shown to affect the concentrations of various ions in the soil; this may further influence nutrient absorption from the soil to plant roots, which can be referred to as the AR-soil chemical characteristics-plant relationship. Most researchers have demonstrated that acid deposition accelerates the leaching of base cations and that long-term ion leaching leads to a nutrient deficiency in the soil (Qiu et al., 2015; Nawaz et al., 2012).

Nitrogen deposition can increase cation leaching from forest soils, lower the soil buffering capacity, and contributes to soil acidity in two ways: (1) from the direct effects of nitric acid and (2) the nitrification of ammonia in soil, which can generate H^+ ions (Bolan et al., 2004; Blanco et al., 2012) (Fig. 2(6)). Acidic soil could change the soil environment and affect plant growth and metabolism, such as by reducing the availability of essential nutrients (e.g., P and N) and increasing the availability of heavy metals (e.g., cadmium and lead) (Fig. 2 (7)). Moreover, excessive soil N increases the leaching of base ions, resulting in a forest nutrient imbalance, which leads to forest decay.

The overall effect of AR on the storage of soil organic matter, such as organic carbon (OC) and organic nitrogen (ON) (Fig. 2(8)), as well as the circulation of essential nutrients, depends on the amount of acid deposition and the different types of forests (Ouyang et al., 2008). Long-term exposure to AR may promote the accumulation of OC in the soil, which may be attributed to the inhibition of microbial decomposition of OC (Wu et al., 2016). The effects of AR or acid deposition on OC and ON may further affect their interactions with microorganisms.

Acid rain may cause excessive leaching of H^+ in soil, and this exceeds the buffer capacity of many soils, thus adversely affecting plants. Plant leaves intercept most of AR; however, the percolation of AR into the soil can affect plant roots (an AR-soil chemical characteristics-plant pathway). Some reports have suggested that acidified soil may limit plant growth simply because H^+ is toxic to roots (Ramlall et al., 2015).

4.1.2. Soil salt leaching effects

Acid rain penetrates through soil particles, washing away the basic cations of the soil, which are replaced by other acidic cations such as H^+, aluminium ions (Al^{3+}), and Mn^{2+}, which in turn cause problems related to soil acidification (Bolan et al., 2001; Seguel et al., 2013; Miransari, 2014). Among them, the increase in the concentration of Al^{3+} in soil solution, combined with the action of soil acidification, causes low productivity of plants and directly or indirectly affects the N cycle, N fixation, and the absorption of available phosphorus (P), which harms plant physiology and growth (Maltz et al., 2019) (Fig. 2(9)).

In the process of nutrient leaching and the acidification of soil, the heavy metal ions mobilized by acid deposition, including the content, speciation, composition, and bioavailability of the ions in the soil, will also be affected. For example, excess Mn^{2+} and low pH significantly reduced CAT activity in cucumber roots (Shi et al., 2006). Cadmium (Cd^{2+}) is one of the most toxic elements when present in the soil. In combined treatments, a high concentration of Cd^{2+} (100 mg/kg) and low pH 3.0 caused by AR can decrease the total biomass of plants and change the biomass allocation into different plant organs (Choppala et al., 2014). The other combined treatments in a high concentration of Cd^{2+} and with AR reduced the content of Fe^{3+} and Mg^{2+} in the soil while further inhibiting photosynthesis and reducing biomass (Shi et al., 2006).

4.2. AR-soil microorganisms-plant

Previous studies show that microbes influence plant survival and growth. For example, microorganisms in the rhizosphere can regulate soil N and cause plants to secrete plant hormones, such as indoleacetic acid, to regulate plant growth and flowering (Lu et al., 2018). Moreover, the interactions between plants (e.g., agricultural crops) and their symbiotic microbes have been enhanced by long-term co-evolution, which allows them to adapt to environmental changes and stress conditions (Turkovskaya and Golubev, 2020; Chen et al., 2021). Acid rain-soil microorganisms-plant interaction is another important pathway that indirectly affects plants. The H^+ in SAR is toxic to soil microorganisms and roots (Chen et al., 2012; Yu et al., 2017). With large amounts of H^+ ions permeating the soil, decreases in the activity, community structure, and functional diversity of the soil microbial community may further affect plant physiological activities (Shu et al., 2019; Liu et al., 2020a).

Acid rain can negatively affect soil bacterial diversity, biomass, and functions. For example, AR may substantially alter soil microbial biomass (Liu et al., 2020b), while a high frequency of AR significantly decreases soil microbial biomass, especially for gram-negative bacteria in the forest soil (Liu et al., 2021c). The microbial biomass of both C and N decreases with excessive nitrogen deposition, as studied in subtropical forests (Lv et al., 2014; Tian et al., 2018). Acid rain can affect the survival of soil rhizobia and soil nitrogen-fixing bacteria (SNB), thus impacting plant performance (Wang et al., 2017) (Fig. 2(10)).

The AM fungi can cause a positive effect on plant N fixation and the absorption of available P to some extent (Maltz et al., 2019). However, environmental stress caused by strong acids may hinder this process and interrupt both plant and fungal growth (Chaudhary and Dick, 2016; Maltz et al., 2019), thus affecting the absorption of available P from the soil in

the roots of plants (Fig. 2(11)). Additionally, plants showed different responses to AR through symbiosis with different types of mycorrhizal fungi. The meta-analysis indicated that plants with a symbiotic relationship with different mycorrhizal types exhibited a difference in their traits or responses to the acidity of AR treatment (Figs. 4 and 5). Previous studies have shown that plants inoculated with either AM or EcM fungi can effectively increase the resistance of specific plants to AR stress (Li et al., 2019; Wang et al., 2021). For example, EcM fungal inoculation could alleviate the negative effects of AR on the process of N-cycling by microbes in forest soils by enhancing substrate availability (Li et al., 2019) (Fig. 2(12)). However, AM fungi seem to be more vulnerable to acidic soil (Liu et al., 2017), which is less conducive to assisting plant growth and nutrient absorption compared to EcM plants (see the nearly neutral overall effects of treatment pH on EcM plants in Figs. 4 and 5). EcM plants may gain both physical and chemical shielding effects from the mycelial structure through symbiosis with ectomycorrhizal fungi (Courty et al., 2010; Martino and Perotto, 2010), which may explain the divergent roles of AM and EcM in mediating the effects of AR on plants.

The relationship between soil microbes, plants, and AR is complex. A few studies have also shown that some plant-associated microorganisms are eosinophilic because they can adapt to specific acidity levels and become more active with AR in some instances; thus, AR further promotes plant performance (Zeng et al., 2018). We recommend giving more attention to the effects of AR on plant microorganism symbiosis (e.g., soil nitrogen-fixing soil bacteria, AM, and EcM fungi) with the pathways in which AR indirectly affects plants.

5. Conclusions and perspectives

The study of the effects of AR on soil-plant system is an important research topic worldwide related to how plant performance and productivity respond to stress created by lowering acidity. In this overview, the direct effects of AR on plants and the indirect effects of AR-soil chemical characteristics/soil microorganisms-plant are summarized and analyzed to provide more comprehensive perspectives for further study. We showed evidence of the direct effects of AR on plant performance and reproduction, in line with the previous studies. We also showed that AR indirectly affects plants by modifying soil chemical properties and microbial composition pathways. We advocate that further investigations should focus on the following:

(1) The relationship between AR-rhizosphere microorganisms-plant as rhizospheric microorganisms can provide relative advantages to help their hosts (Qu et al., 2020; Turkovskaya and Golubev, 2020), which may offset the adverse effects of AR. In addition, AR disrupts the distribution, composition, and function of rhizosphere microorganisms, which may harm plant performance and their adaption to the environment.
(2) The indirect effects of AR on plants, such as AR-soil acidification-plant internal nutrient cycling in ecosystem carbon and nitrogen cycling.
(3) Investigating the combined effects of AR and heavy metals on plants. How do AR and heavy metal additives affect plants in polluted soil? For instance, the combined effects of lanthanum chloride ($LaCl_3$) and AR on plants need further study (Zhang et al., 2017).

CRediT authorship contribution statement

Yan Zhang: Conceptualization, Writing - Original draft preparation. Jiahong Li: Writing- Original draft preparation. Junyan Tan: Writing - Original draft preparation. Wenbin Li: Writing - Original draft preparation. Bhupinder Pal Singh: Writing - Review & Editing. Xunan Yang: Writing - Original draft preparation. Nanthi Bolan Interpretation of the discussion of various sections and provided critical revision and editing of the article. Xin Chen: Writing - Original draft preparation. Song Xu: Writing - Original draft preparation. Yanping Bao: Writing - Original draft preparation. Daofei Lv: Writing - Original draft preparation. Anan Peng: Writing - Original draft preparation. Yanbo Zhou: Writing - Original draft preparation. Hailong Wang: Conceptualization, Interpretation of the discussion of various sections and provided critical revision and editing of the article.

Data availability

Data will be made available on request.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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